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RESEARCH PAPER

The lowland seasonally dry subtropical forests in central Argentina: vegetation types and a call for conservation

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Abstract

Aims: The native woody vegetation from the Espinal phytogeographic province in central Argentina, found in subtropical-warm temperate climates, represents part of the southernmost seasonally dry forest in South America. Although this vegetation has been studied for over a century, a complete phytosociological survey is still needed. This lack of knowledge makes its spatial delimitation and the establishment of efficient conservation strategies particularly difficult. The main goals of this study were to classify these forests and assess their current forest cover and to better define the extent of the Espinal phytogeographic province in Córdoba region, central Argentina. **Study area:** Espinal Phytogeographic Province in Córdoba region, central Argentina (ca. 101,500 km^2). **Methods:** We sampled 122 stands following the principles of the Zürich-Montpellier School of phytosociology; relevés were classified through the ISOPAM hierarchical analysis. The extent of the Espinal phytogeographic province was established by overlaying previous vegetation maps, and a map showing the current distribution of forest patches was constructed based on a supervised classification of Landsat images. **Results:** Four woody vegetation types of seasonally dry subtropical forest were identified based on the fidelity and the abundance of diagnostic species: (1) *Aspidosperma quebracho-blanco* forest; (2) *Zanthoxylum coco* forest; (3) *Geoffroea decorticans* forest; and (4) *Prosopis caldenia* forest. These vegetation types were segregated along gradients of temperature and precipitation seasonality and soil-texture and sodium content. The remaining forest patches represent 3.43% of the extent of the Espinal province in Córdoba region of which only 1.05% is represented in protected areas. **Conclusions:** We present a classification of the Espinal forest based on a complete floristic survey. Despite the dramatic forest loss reported, our results show that some forest patches representative of the Espinal are still likely to be found in the area. However, urgent measures should be taken to establish new protected natural areas in order to preserve the last remaining forest patches.

Taxonomic reference: Catálogo de las Plantas Vasculares del Cono Sur (Zuloaga et al. 2008) and its online update (http://www.darwin.edu.ar).

Abbreviations: ISOMAP = isometric feature mapping; ISOPAM = isometric partitioning around medoids.

Keywords

central Argentina, chorotype, diagnostic species, dry subtropical forest, Espinal phytogeographic province, exotic species, floristic survey, gradient analysis, vegetation classification, vegetation map, vegetation plot, woody vegetation

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Introduction

Dry tropical and subtropical forests are a potentially extensive set of types in South America (DRYFLOR et al. 2016; Kuemmerle et al. 2017) and are among the most threatened ecosystems in the world, with ca. 10% of their original extent remaining (Bastin et al. 2017). While dry tropical forests have received more attention (Pennington et al. 2000; Linares-Palomino et al. 2015; Dexter et al. 2018), the knowledge of subtropical-warm temperate dry forests distribution and composition is locally fragmented or focused only on woody species instead of on complete floristic inventories (Lewis et al. 2009; Kuemmerle et al. 2017; Silva de Miranda et al. 2018).

Among the seasonally dry subtropical forests in South America the southernmost ones are included in the Espinal phytogeographic province (Cabrera 1976; Morrone 2001) and their phytosociological knowledge is perhaps one of the poorest in the region. The Espinal was distinguished from the Chaco and Pampa phytogeographic provinces for the first time by Cabrera (1953, 1976), who recognized it as a phytogeographic province within the Chaquenian Dominium in Argentina. In addition, Cabrera (1976) defined the Espinal as an "impoverished Chaco" due to the lack of several dominant trees, mainly *Schinopsis lorentzii* and *S. balansae* (i.e, red quebrachos) and a lower tree canopy (Bucher 1982; Cabido et al. 2018). These differences in floristic composition and physiognomy may be due to changes in temperature (mainly a decrease in annual mean temperature and an increase in frost frequency) in the Espinal as a consequence of the increase in latitude (Bucher 1982; Morello et al. 2018).

Currently, the prevailing vegetation of the Espinal is a mosaic of xerophytic deciduous to semi-deciduous forests and shrublands intermingled with grasslands and savanna-like parklands distributed mostly in central and eastern Argentina and, to a lesser extent, in Uruguay and Brazil (Lewis and Collantes 1973; Cabrera 1976; Morello et al. 2018; Oyarzábal et al. 2018). However, given the great extension of the Espinal area (ca. 288,000 km^2; Mateucci 2018), especially in the North-South direction, it shows climatic gradients, including a warmer subtropical and humid climate in its northern extreme, while to the south and west the prevailing climate is warm temperate and dry with marked water deficits (Cabido et al. 2018; Matteucci 2018). This gradient is coupled also with changes in soils with increasing sand content and soil drainage towards the southern extreme (Gorgas and Tassile 2006). This environmental variability results in changes in floristic composition and physiognomy recognized by different authors (Lewis and Collantes 1973; Cabrera 1976; Cabido et al. 2018). Lewis and Collantes (1973) provided the most exhaustive description of the Espinal native vegetation, and identified different units (i.e. districts) based on the physiognomy of the vegetation and the relative abundance of some ubiquitous species of *Prosopis* as well as *Celtis ehrenbergiana* and *Geoffroea decorticants*. Lewis et al. (2009) described the structure of selected tree and shrub populations in several Espinal forest relicts located in a relatively small area, while Noy-Meir et al. (2012) provided complete floristic relevés (comprising both woody and herbaceous species), but restricted to a single remnant patch. Recently, Cabido et al. (2018) reported a classification of woody vegetation in central Argentina and included all Espinal forests in a single vegetation type. Apart from these contributions, there is still lacking a detailed characterization based on a comprehensive phytosociological analysis that includes all vascular plants of the Espinal forest remnants and their relations with environmental determinants.

Historically, the Espinal phytogeographic province was largely forested. Since the beginning of 20th century, these forests have been under heavy pressure (Schofield and Bucher 1986; Boletta et al. 2006; Guida-Johnson and Zuleta 2013; Agost 2015), mainly because the area comprises some of the most suitable soils for agriculture and cattle grazing in the world (Blum and Swaran 2004; Blum 2013). Decades of exploitation driven mainly by timber and firewood extraction (Schofield and Bucher 1986), jointly with the expansion of agribusiness (Arturi 2005; Guida-Johnson and Zuleta 2013; Fehlenberg et al. 2017), have led to the devastation of most of the Espinal forests. Now, only isolated relicts remain (Lewis et al. 2006; Agost 2015; Garachana et al. 2018). These remnants of native woody patches are also threatened by the establishment of several exotic shrub and tree species (Lewis et al. 2004; Giorgis and Tecco 2014; Cabido et al. 2018). These disturbances have resulted in changes in the provision of ecosystem goods and services such as water cycle regulation (Jobbagy et al. 2008), carbon stock (Conti and Díaz 2013) and pollination (Dicks et al. 2016). In addition to the dramatic reduction in Espinal forests, the full extent of protected areas created through official agreements represents only a small fraction of the Espinal in Argentina (ca. 0.03% according to Brown et al. 2006 and Matteucci 2018). Worse, there has been a lack of agreement concerning the real extent of the Espinal phytogeographic province (Lewis and Collantes 1973; Cabrera 1976; Cabido et al. 2018; Morello et al. 2018; Oyarzábal et al. 2018), resulting in maps portraying different sizes, shapes and boundaries; recently Arana et al. (2017) even included the Espinal in the Pampean phytogeographic province. All these issues call for an urgent and detailed description of the main vegetation types combined with an assessment of the current distribution of the Espinal forest remnants.

A great area of the Espinal phytogeographic province occurs in Córdoba province (hereafter, Córdoba region), central Argentina (Matteucci 2018), comprising an outstanding representation of the whole phytogeographic province (Lewis and Collantes 1973; Cabrera 1976). Most of the vegetation types described previously by different authors (Lewis and Collantes 1973; Cabrera 1976) can still be found in Córdoba. The recent paper by Cabido et al. (2018) reported the woody vegetation types for the whole Córdoba region, identifying a single type within the Espinal (i.e. Type 1.3 *Prosopis nigra – Celtis ehrenbergiana – Prosopis caldenia* in Cabido et al. 2018), but recognizing its internal heteroge-

neity. Therefore, the main goal of our study is to expand the classification reported by Cabido et al. (2018) describing the remaining native vegetation types and to assess the spatial extent of the Espinal in Córdoba region, central Argentina. Specifically, our aims were to: (1) classify and characterize the woody native patches of the Espinal based on complete vascular plant surveys; (2) analyze the relationships between the obtained vegetation types and the main regional bioclimatic and edaphic variables; and (3) construct a map of the extent of Espinal phytogeographic province in Córdoba region and assess the current woody vegetation distribution. Additionally, we estimate the area of woody patches of the Espinal in Córdoba region currently included under formal protection (i.e. protected natural areas).

Study area

Currently, the whole distribution area of the Espinal forests is reduced to small and isolated remnants of native woody patches (Cabido et al. 2018; Garachana et al. 2018; Matteucci 2018) in an agricultural matrix, mainly soybean, maize, wheat, sunflower and peanut, with scattered pastures for livestock grazing (mainly cattle). In Argentina, the Espinal phytogeographic province forms a sub-circular belt extended in the central and eastern part of the country; our study area was restricted to the Espinal comprising the lowlands in the central, eastern and southern part of Córdoba region, central Argentina (Figure 1A). The latitude ranges from 30.47° to 34.98°S, while longitude varies from 62.22° to 65.08°W. This area belongs to the Espinal phytogeographic province that borders the dry Chaco forests to the north and the low mountain Chaco vegetation (i.e. sierra Chaco) to the west, and forms a complex and progressive transition towards the Pampa grasslands to the south and east of the province (Figure 1B; Lewis and Collantes 1973; Cabrera 1976). This area occupies the southwestern sector of the Chaco-Pampean geomorphological province (Carignano et al. 2014), comprising two main units: the fluvio-eolian plain, located to the north and east of the study area, and the sandy plain to the southwest of the province. Opposite to tropical ecosystems, in subtropical forests in Argentina, winter and summer seasons are differentiated and freezing is likely to occur, showing a markedly thermal seasonality (Morello et al. 2018). In the study area climate varies from subtropical in the northern extreme to warm temperate in the most southern part (Capitanelli 1979; Matteucci 2018; see climate diagrams in Figure 1B). Rainfall is largely concentrated in the warm season, from October to March, with total annual rainfall ranging from 600 mm (southwestern extreme) to 900 mm (northeastern sector), while the annual mean temperature increases from 16.0 to 17.6 °C in the same direction (De Fina 1992).

Methods

Vegetation data

The vegetation survey was carried out throughout the study area, covering the geographic, topographic and

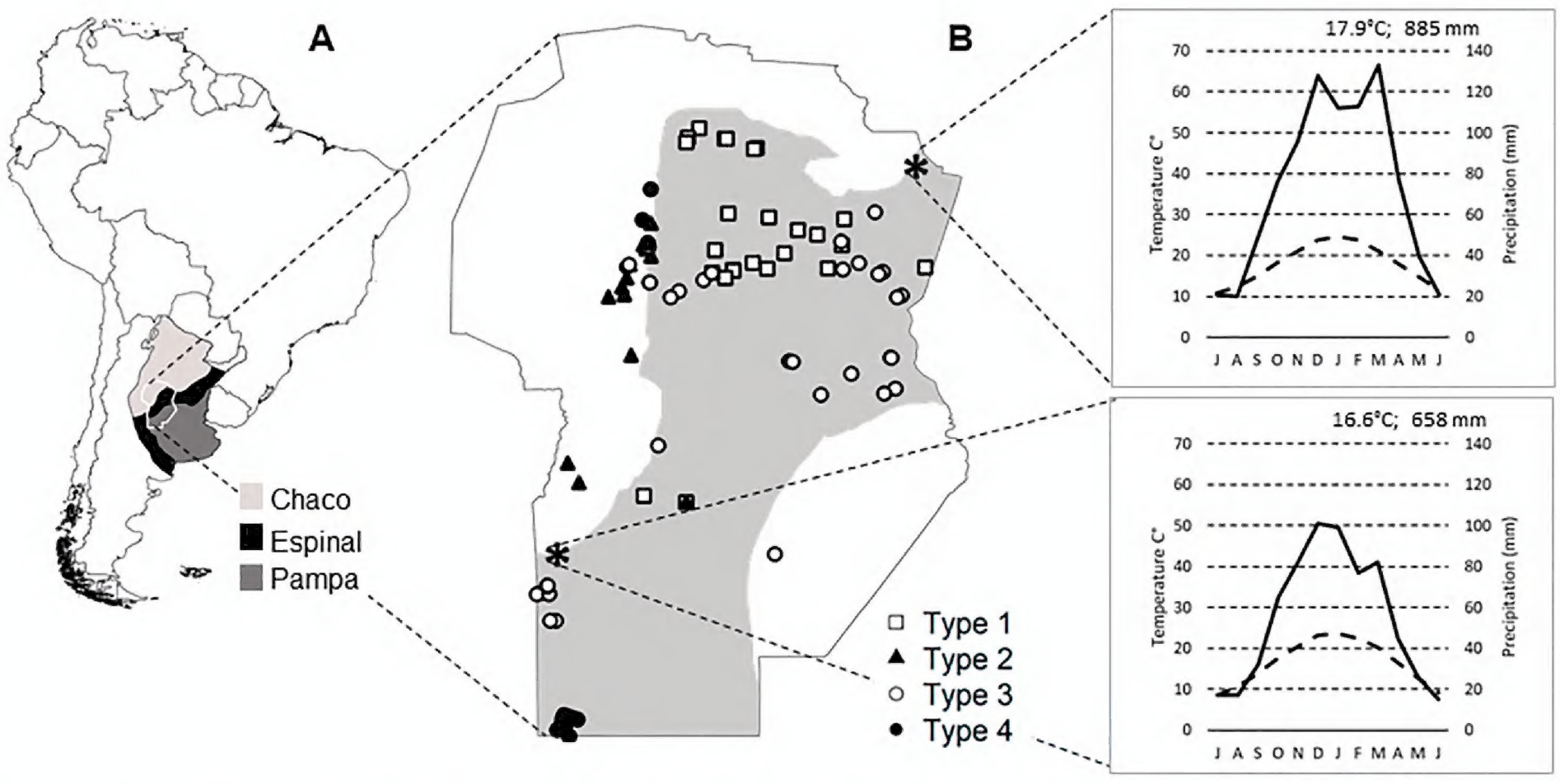

Figure 1. A Location of Córdoba region and Argentina in South-America, showing the location of Espinal, Chaco and Pampa phytogeographic provinces in Argentina based on Cabrera (1976); **B** distribution of sample plots (relevés) in Córdoba region discriminating the four vegetation types: 1) *Aspidosperma quebracho-blanco* forest; 2) *Zanthoxylum coco* forest; 3) *Geoffroea decorticans* forest; and 4) *Prosopis caldenia* forest. In grey, Espinal extent in Córdoba region according to Lewis and Collantes (1973). Two climatic diagrams (see asterisks) representing the northern and southern extremes of the study area are included in the figure (climatic data were obtained from WorldClim database).

ecological variability of the Espinal forests. Sampling followed the Zürich-Montepellier School of phytosociology (Braun-Blanquet 1932). In order to take into account the physiognomic heterogeneity of the vegetation, both conserved and disturbed forests were sampled. Riparian vegetation and grasslands, as well as patches dominated by exotic tree species (with an exotic tree cover of more than 20%) were not considered. Since different authors propose different boundaries for the Espinal phytogeographic province, the vegetation survey was carried out not only in the Espinal area indicated in Figure 1B (Lewis and Collantes 1973), but also in areas included in the Espinal by other authors (Cabrera 1976; Cabido et al. 2018; Morello et al. 2018; Oyarzábal et al. 2018). Our sampling comprised 122 georeferenced 20 m × 20 m plots; 64 samples had already been used for a previous analysis by Cabido et al. (2018), and the additional 58 corresponded to original unpublished data. In each plot, vascular plants were recorded and species cover was estimated using the cover-abundance scale of Braun-Blanquet (1932). The height and cover of the tree, shrub and herb layers were visually estimated. Data were collected during the growing season (summer of Southern Hemisphere) from 2010 to 2019. Endemic taxa at the national level followed Zuloaga et al. (1994, 2008), Cabido et al. (1998), Zuloaga and Morrone (1999a, 1999b) and Chiapella and Demaio (2015), while species nomenclature and their distributional range followed the catalogue of vascular plants of the Southern Cone (Zuloaga et al. 2008) and its online update (http://www.darwin.edu.ar/). All vegetation plots are registered in the Global Index of Vegetation-Plot Database (Dengler et al. 2011; http://www.givd.info) under ID SA-AR-002 (see also Suppl. material 1: Table S1.1).

To assess the main trends of species distribution patterns and the way in which these trends are represented in the different vegetation types, species chorotypes (groups of species with a similar distribution) were assigned following the criteria of Cabido et al. (1998): Southern-brazilian (1), Chaquenian (2), Low montane (3), Patagonian (4) and Exotic (5). The Southern-brazilian chorotype includes species widely distributed through the lowlands of central and north-eastern Argentina, and in the adjacent territories of Paraguay, Brazil and Uruguay. They may also reach the mountains but sharply decline in number above 1,000 m a.s.l. The Chaquenian chorotype comprises species distributed mainly through the dry Chaco lowland territories of central and north-western Argentina and the whole Chaco-Pampean plain. The Low montane chorotype includes species distributed at low altitudes (lower than 1,500 m) in extra-Andean Mountains of central and north-western Argentina and Bolivia. The Patagonian chorotype species are characterized by ranges extending over the whole Patagonian phytogeographic province, both in Andean and extra-Andean habitats. The Exotic chorotype includes species introduced to Argentina from other areas of the world. For each vegetation type, mean percentage of each chorotype per plot as well as the mean species richness and number of exotics per plot were calculated. Further, species were sorted into life forms as: cactus (c), climber (cl), epiphyte (e), fern (f), grass (g), graminoid (gr), herb (h), succulent herb (hs), parasite (p), palm (pl), shrub (s), subshrub (ss), succulent shrub (rs) and tree (t). The classification of life forms followed previous surveys in central Argentina, slightly modified from Giorgis et al. (2005) and Zuloaga et al. (2008).

Environmental variables

Bioclimatic variables and altitude (Alt) were taken as interpolated values from the WorldClim database (http://www.worldclim.org; Hijmans et al. 2005), at a spatial resolution of 2.5 arc-minutes for continental South America. The bioclimatic variables selected were annual mean temperature (AMT), temperature seasonality (TS), temperature annual range (TAR), precipitation seasonality (PS), precipitation of the warmest quarter (PWaQ), annual precipitation (AP), and precipitation of the driest month (PDM) (see O'Donnell and Ignizio 2012 for details concerning all the bioclimatic variables). These bioclimatic variables were selected because the main climatic constraints for the vegetation in the study area have been shown by Matteucci (2018) to be temperature and precipitation seasonality. In order to obtain data on edaphic variables (i.e. soil type, organic matter, pH, soil depth, clay, lime, fine sand, coarse sand and sodium percentage) for each plot, all the 122 relevés were plotted on digitalized maps of the soils of Córdoba region constructed at the scale of 1:500,000 and 1:50,000 (Gorgas and Tassile 2006; http://visor.geointa.inta.gob.ar/?p=857). The map at the scale 1:50,000 was preferentially used, but since this map still has some gaps (areas not covered at this scale) we completed the data with the map at the scale of 1:500,000. These maps depict soil cartographic units and describe the internal heterogeneity of each unit through representative soil profiles providing results of analysis of their chemical and physical properties.

Spatial analysis: Espinal extent, current woody vegetation distribution and representation on protected areas

In order to establish the extent of the Espinal phytogeographic province within Córdoba region, all available maps by different authors and dates, were overlapped in QGIS (QGIS Development Team 2019) under the same projection system (WGS84). The maps by Lewis and Collantes (1973), Cabido et al. (2018) and Morello et al. (2018), were manually digitalized while the other maps by Cabrera (1976) and Oyarzábal et al. (2018) were available online. The area covered by the overlapping of the different maps was defined as the extent of the phytogeographic province. Since the areas depicted for the Espinal by the different authors differed substantially, their representativeness with respect to the Espinal in the overlapped map was estimated. By means of this procedure, we aimed to

highlight the difficulties of establishing the boundaries of the Espinal when using only the map of any single author.

The area covered by current woody vegetation forest patches was estimated within the overlapped map showing the Espinal extent. Cloud free Landsat 8 OLI data processed to level L1T were acquired from the United States Geological Survey (USGS; http://earthexplorer.usgs.gov/) to assess and map the current distribution of the Espinal woody patches. The spectral bands used in this study included blue (0.45–0.51 μm), green (0.53–0.59 μm), red (0.64–0.67 μm), and near infrared (0.85–0.88 μm). Digital numbers of the Landsat imagery were converted to top-of-atmosphere reflectance according to the instructions provided by the USGS. Ten scenes of this satellite were used to cover the entire area of the Espinal forest in Córdoba region (path 228–229 and row 081, 082, 083, and 084). For each scene, images from April and September 2016 were used. Numerous sites selected during field reconnaissance and high-resolution images in Google Earth were used as the training sites for the supervised classification of the image. The supervised classification of images was performed through Support vector machines (all digital processing was performed using the ENVI (EX 2009) and QGIS software). To reach adequate results, different successive classifications were necessary, masking areas or adding, combining and removing training sites. Post processing was performed by correcting classification inaccuracies and by reducing salt-and-pepper noise, partially due to the high degree of fragmentation of natural vegetation in the study area.

Finally, to assess the actual woody cover of the Espinal area included in the current protected areas system, the boundaries of the natural protected areas were overlapped on the current vegetation map using the shapes of the protected areas obtained from the Argentinean Secretary of Environment and Sustainable Development (https://www.argentina.gob.ar/ambiente/tierra/protegida/mapa), and the Environmental Provincial Secretary.

Data analyses

The ISOmetric feature mapping and Partition Around Medoids (ISOPAM) ordination and classification method was employed to analyze the 122 plots × 616 species matrix. This analysis was used to detect the major vegetation types and their corresponding diagnostic species groups (Schmidtlein et al. 2010; Černý et al. 2015). The ISOPAM is based on the classification of ordination scores from isometric feature mapping (Tenembaum et al. 2000) in which the ordination and partitioning are repeated searching for partitions for maximum discrimination of vegetation units with high overall fidelity of species to groups until a pre-defined stopping criterion is met (e.g., G statistic and number of clusters; Schmidtlein et al. 2010). Hierarchical ISOPAM was run on the Bray-Curtis dissimilarity matrix. This matrix was constructed with the floristic table after transformation of Braun-Blanquet scores to central class values. The maximum number of clusters on each hierarchical level was arbitrarily set to 10 and standardized G statistics to 5. For each vegetation type, diagnostic species were selected using the phi coefficient of fidelity (Chytrý et al. 2002). Those species with phi > 0.1 and a statistically significant ($p < 0.01$) association with a particular vegetation type according to Fisher's exact test, were considered as diagnostic. These analyses were performed in the JUICE 7.0 program (Tichý 2002). Each vegetation type was named after species with: 1) phi > 0.2 and a statistically significant ($p < 0.01$) association with a given vegetation type; and 2) constancy > 50%. The vegetation matrix was ordinated through isometric feature mapping (ISOMAP; Tenembaum et al. 2000; Černý et al. 2015), using the number of neighbors to the optimal value from the first hierarchical level of the ISOPAM classification. All bioclimatic data extractions were conducted using the *extract* function on R *version* 3.5.1 (R Core Team 2018). Environmental and edaphic variables with the highest squared correlation coefficient were related to the ISOMAP ordination through the *envift* function from the vegan R-package (http://CRAN.R-project.org/package=vegan). In order to evaluate the differences in mean percentage of each chorotype per plot as well as the differences in the mean species richness and of exotics per plot among the four vegetation types, ANOVAs were performed in R software. Before conducting the analysis, the normality of the data and the homoscedasticity of variances were evaluated and when these requirements were not accomplished the data were natural log transformed.

Incidence-based rarefaction and extrapolation (R/E) curves using sample size-based and coverage-based methods were performed to evaluate whether plant species from the different vegetation types classified by the ISOPAM method were well represented (Budka et al. 2018). Chao2, Jackknife 1 and Jackknife 2 non-parametric estimators for incidence data were used to estimate the total number of species that would be present in each vegetation type. Non-parametric estimators for incidence data, and incidence-based rarefaction and extrapolation (R/E) curves were performed using the *SpadeR* and *iNEXT* R-packages (Chao and Chiu 2016), respectively.

Results

Floristic composition of vegetation types

The overall number of species recorded was 616 (38 trees, 65 shrubs and 513 belonging to other life forms), comprising 86 families and 353 genera. *Poaceae* (102 species), *Asteraceae* (100), *Fabaceae* and *Solanaceae* (32 species each), *Malvaceae* (31) and *Euphorbiaceae* (24) comprised 52.11% of all encountered species. The most taxonomically diverse genera were: *Solanum* with 14 species, *Baccharis* with 12 species, *Setaria* with 11 species, *Prosopis* and *Nassella* with nine species each, *Euphorbia*, *Lycium* and *Tillandsia* with eight species each, and *Cyperus* and *Opuntia* with six species each. In the 122 stands sampled we

recorded 116 endemic taxa at the national level and 67 exotic species (Table 1; see also Suppl. material 2: Table S2.1 for the extended Table 1).

Table 1. Shortened synoptic table obtained through the ISOPAM classification showing the identified vegetation types along with the percentage constancy and mean Braun-Blanquet cover values based on 122 relevés collected in the Espinal phytogeographic province in Córdoba, central Argentina. Species are sorted by decreasing fidelity within each vegetation type. Dark, medium and light grey indicate phi > 0.2, phi > 0.15 and phi > 0.1, respectively. Only those species with phi ≥ 0.1 in at least one forest type were included in the table. Vegetation types are: 1, *Aspidosperma quebracho-blanco* forest; 2, *Zanthoxylum coco* forest; 3, *Geoffroea decorticans* forest; and 4, *Prosopis caldenia* forest. LF, Life forms: c, cactus; cl, climber; e, epiphyte; f, fern; g, grass; gr, graminoid; h, herb; hs, succulent herb; p, parasite; pl, palm; s, shrub; ss, subshrub; rs, succulent shrub; t, tree. CT, chorotype: 1, Southern-brazilian; 2, Chaquenian; 3, Low montane; 4, Patagonian; 5, Exotic. Symbols: †, endemic species at the national level.

Vegetation type			1	2	3	4
Number of relevés			29	22	50	21
Species	**LF**	**CT**				
Aspidosperma quebracho-blanco	t	2	76[3]	55[2]	2[1]	
Porlieria microphylla	s	2	100[2]	59[1]	2[1]	5[+]
Senegalia praecox	t	2	38[2]	45[2]		
Celtis ehrenbergiana	t	1	100[3]	95[2]	76[2]	86[1]
Zanthoxylum coco	t	3		73[2]	4[2]	
Oplismenus hirtellus	g	1		41[2]	2[1]	
Leonurus japonicus	h	5	7[1]	45[2]	12[+]	24[1]
Chromolaena hookeriana	s	3	17[+]	55[2]		
Ipomoea purpurea	cl	1	14[+]	64[2]		
Lithraea molleoides	t	3		50[2]		
Condalia buxifolia	t	3		27[2]		
Melinis repens	g	5		14[2]		
Croton lachnostachyus	s	3	14[1]	82[1]		
Schinopsis lorentzii	t	1		9[2]		
Mandevilla pentlandiana	cl	1	7[+]	73[1]		
Lorentzianthus viscidus	s	3		59[1]	2[+]	
Colletia spinosissima	s	3		9[2]		
Ligustrum lucidum	t	5	7[+]	55[1]	2[1]	
Gouinia latifolia	g	2	14[1]	45[1]		
Paspalum malacophyllum	g	1		18[2]		
Flourensia thurifera†	s	3		14[2]		
Passiflora morifolia	cl	1	3[+]	50[1]		
Euphorbia berteroana	h	2	3[+]	45[1]		
Condalia montana†	t	3	3[+]	27[1]		
Ruprechtia apetala	t	3		27[1]		
Geoffroea decorticans	t	2	79[1]	50[2]	90[3]	81[2]
Cynodon dactylon	g	5	14[1]	9[2]	38[2]	24[1]
Sida rhombifolia	ss	1	41[1]	77[1]	72[2]	10[+]
Sporobolus spartinus	g	2			16[2]	
Prosopis caldenia†	t	2			10[2]	90[3]
Jarava pseudoichu	g	3	17[2]	50[1]	20[1]	81[4]
Exhalimolobos weddellii	h	1	10[1]	14[+]	4[+]	38[2]
Carex sororia†	gr	1				52[2]
Heterotheca subaxillaris	h	5			2[+]	48[1]
Nassella tenuissima†	g	3		9[1]	6[1]	48[1]
Carduus acanthoides	h	5			6[1]	57[1]
Amelichloa brachychaeta	g	2	7[1]		4[1]	48[1]
Larrea divaricata	s	2	10[+]		2[2]	38[2]
Gamochaeta filaginea	h	1				10[2]

Four main clusters were obtained from the ISOPAM classification, each representing one vegetation type. Although the sample-size-based rarefaction curves showed that the asymptote was not reached for none of the four vegetation types (Figure 2A), the observed species richness reached a high percentage of the species estimated using the non-parametric estimators (see Suppl. material 3: Table S3.1). Further, the coverage-based rarefaction curves suggested that all vegetation types identified were well represented since the sample coverage percentage showed values higher than 0.85 in all types (Figure 2B, C; Suppl. material 3: Table S3.1).

A description of each vegetation type is provided, with reference to its physiognomy (Figure 3), floristic composition (Table 1) and distribution within the study area (Figure 1B):

Type 1. *Aspidosperma quebracho-blanco* forest. Open forest with shrubs, always dominated by a tree layer with a mean cover of 54% ranging from 10 to 90% (see Suppl. material 4: Table S4.1) and a height that may vary from 5 to 15 m. The shrub layer showed mean cover values of 61% with a height ranging from 1.5 to 5 m; the herb layer showed mean cover values of 56%. The diagnostic species were the native trees *Aspidosperma quebracho-blanco* and *Celtis ehrenbergiana*, accompanied by the native shrubs *Porlieria microphylla* and *Senegalia praecox*. In some forest patches, *Prosopis nigra* may reach high cover values.

This type is restricted to the northernmost sector of the area on loessic plains and gentle eastern slopes of the Sierras del Norte on well to excessively drained soils (Enthic Hapludols and Haplustols). A total of 276 taxa were recorded of which 48 species (17.4%) were endemic, while 10 species were found only in this vegetation unit. Twenty three exotic species were recorded, but they had low constancy and cover in all stands.

Type 2. *Zanthoxylum coco* forest. Open low forests with shrubs alternating with patches dominated by closed shrublands. The tree and shrub layers showed mean cover values of 39 and 51% ranging from 5 to 80% and 20 to 90%, respectively. The height of the tree layer ranged from 4 to 15 m. The herb layer showed mean cover values of 56% (see Suppl. material 4: Table S4.1). The diagnostic species included several life forms as trees (e.g., *Zanthoxylum coco*, *Lithraea molleoides* and *Condalia buxifolia*), shrubs (e.g. *Chromolaena hookeriana* and *Croton lachnostachyus*), grasses (e.g. *Oplismenus hirtellus*) and several climbing species (e.g. *Ipomoea purpurea*, *Mandevilla pentlandiana*, *Passiflora morifolia*, among others). In some valley bottoms *Prosopis alba* may reach high cover values.

This vegetation type is distributed on the eastern lower slopes of Córdoba Mountains, in the transitional zone between the Espinal in the lowlands and the proximate area of the Mountain Chaco Forest. Slopes are gentle to steep, with sandy to rocky and excessively drained soils. The total spe-

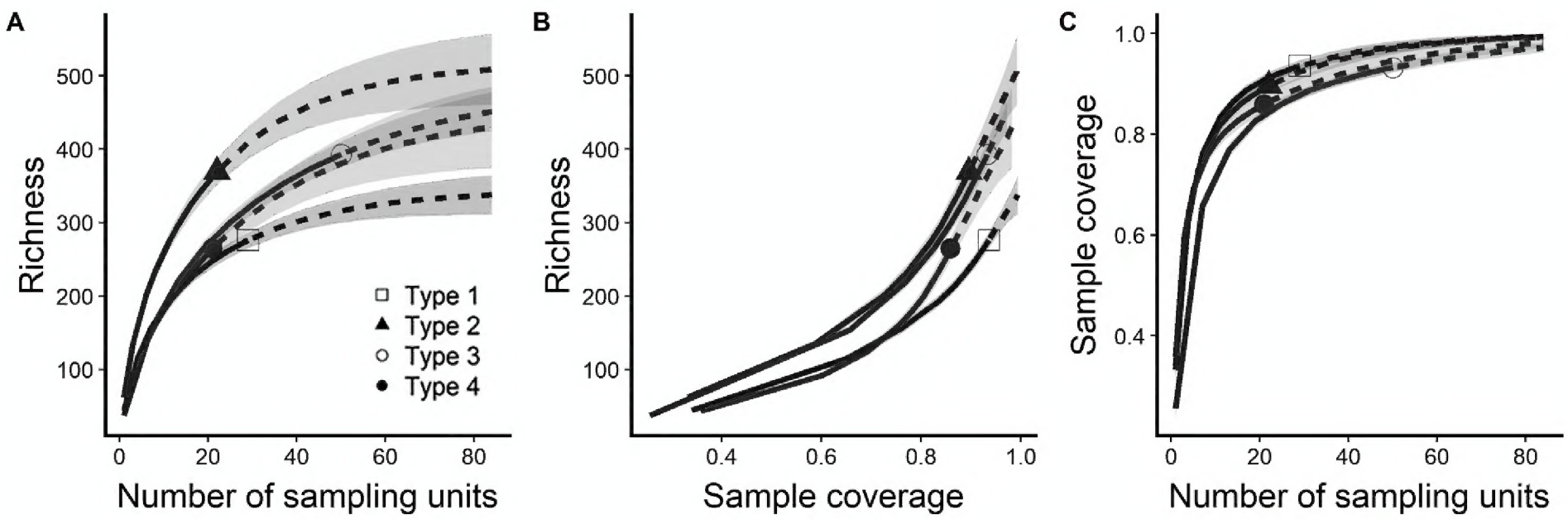

Figure 2. A Sample-size-based and **B** coverage-based rarefaction and extrapolation sampling curves for species richness, and **C** sample completeness curves for each vegetation type. Solid line segments indicate rarefaction and dotted line segments indicate extrapolation (up to a maximum sample size of 80), while shaded areas indicate 95% confidence intervals (based on a bootstrap method with 100 replications).

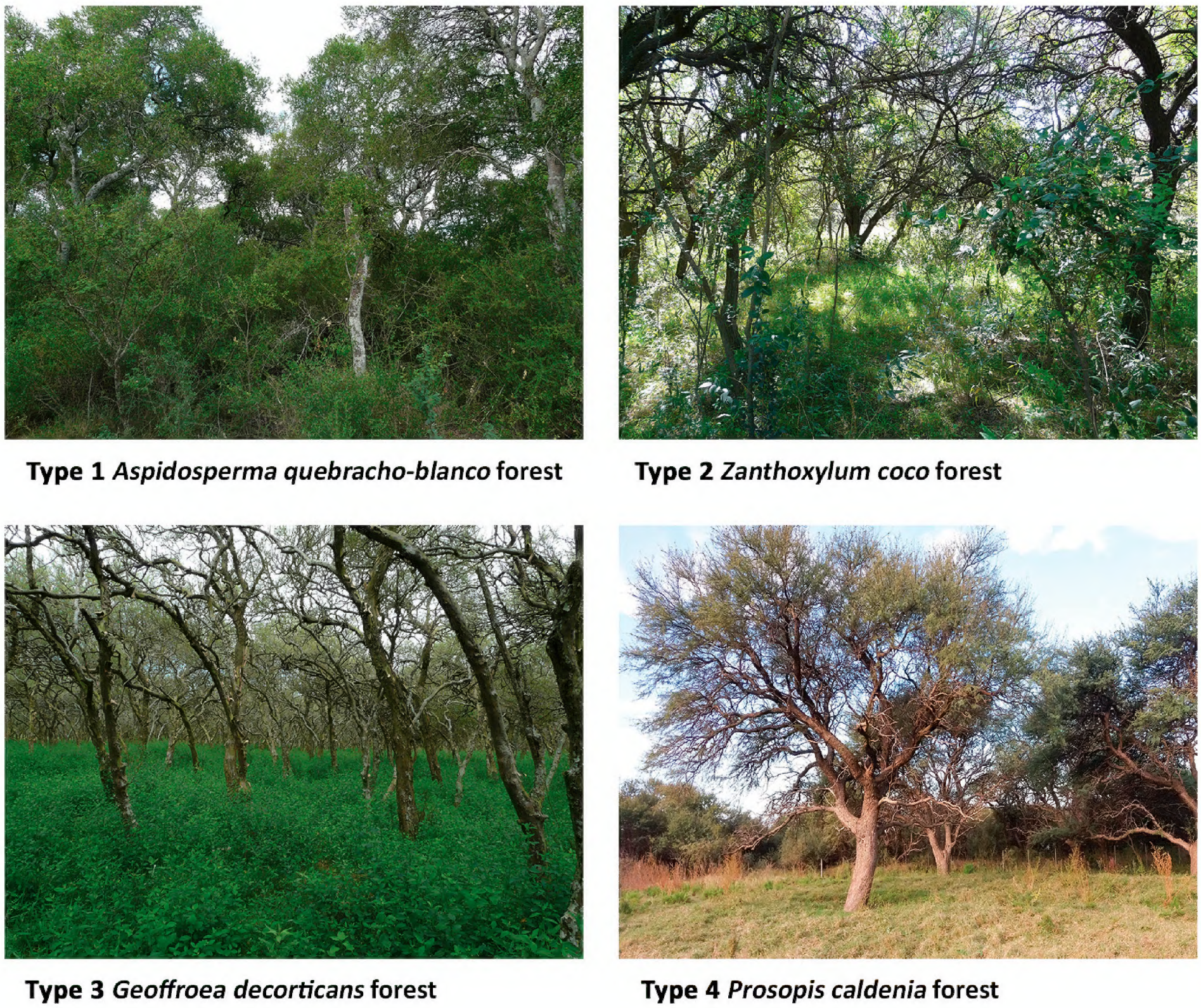
Type 1 *Aspidosperma quebracho-blanco* forest
Type 2 *Zanthoxylum coco* forest
Type 3 *Geoffroea decorticans* forest
Type 4 *Prosopis caldenia* forest

Figure 3. Dominant physiognomy of the four vegetation types described in the Espinal phytogeographic province in Córdoba, central Argentina.

cies richness registered was 369, while the number of endemic species registered was 62 species (16.8%); 11 species were recorded exclusively in this vegetation type. The number of exotic species is relatively low (34 species), but the exotic tree *Ligustrum lucidum* and the exotic herb *Leonurus japonicus* showed high constancy and fidelity to this type.

Type 3. *Geoffroea decorticans* forest. Low open forest with grasses, with well conserved stands intermingled with disturbed patches with lower and more open tree canopy. The tree layer showed a mean cover value of 52% and a height that varied from 4 to 13 m. The shrub and herb layers showed values of 38 and 81%, respectively (see Suppl. material 4: Table S4.1). The diagnostic species were the tree *Geoffroea decorticans*, the grasses *Cynodon dactylon* and *Sporobolus spartinus* and the herb *Sida rhombifolia*. The endemic (Argentina and Uruguay) palm species *Trithrinax campestris* showed its highest relative cover in this vegetation type.

This vegetation type is distributed in the central and eastern part of the study area, on well to moderately well (Haplustols) to imperfectly (Argialbols) drained soils. Differences in soil drainage are associated to internal physiognomic heterogeneity in this type, but also stands in different successional stage may strengthen the internal variability within the *Geoffroea decorticans* forest. A total of 393 species were registered of which 65 (16.5%) were endemics and 11 were recorded only in this vegetation type. Thirty nine species were exotic, with the grass *Cynodon dactylon* showing the highest constancy and relative cover.

Type 4. *Prosopis caldenia* forest. Low open forest with grasses and a tree layer showing a mean cover value of 36% and a height that spans from 5 to 8 m. The shrub layer showed a mean cover of 41%, while the herb layer showed the highest cover value of all vegetation types (93%; see Suppl. material 4: Table S4.1). The diagnostic species were the tree *Prosopis caldenia*, an endemic species from central Argentina, usually associated with *Geoffroea decorticans*, but the latter with low cover values and forming a lower tree layer. In lower and more open canopy sites, patches of grasslands dominated by several diagnostic tussock grasses like *Jarava pseudoichu* and *Nassella tenuissima* can be found.

This vegetation type is restricted to the southern extreme of the study area, on gently undulating sandy plains with lightly to excessively drained soils (Haplustols in gentle slopes; Ustorhtens in sandy summits). This vegetation type showed the lowest species richness (265) of which 47 species were endemic (17.7%) and 18 were registered only in this type. Thirty seven exotic species were recorded; among them, the weeds *Carduus acanthoides* and *Heterotheca subaxilaris* showed high constancy and fidelity to this vegetation type.

Diversity patterns, level of invasion and chorotype distribution across the four forest types

The vegetation types differed in their mean species richness and mean number of exotic species per plot (Figure 4A–B). With 62.1 ± 5.1 species Type 2 (*Zanthoxylon coco* forest) accounted for the highest mean species richness per plot and differed significantly from the other three vegetation types ($F_{(3,118)}$ 12.62; $p < 0.001$). Type 3 (*Geoffroea decorticans* forest) showed the lowest mean species richness per plot (37.4 ±2.2), while Type 1 (*Aspidosperma quebracho-blanco* forest) and Type 4 (*Prosopis caldenia* forest) showed 44.3 ±1.6 and 43.3 ± 2.9 species richness per plot, respectively. The mean number of exotic species per plot varied significantly among vegetation types ($F_{(3,118)}$ 13.96; $p < 0.001$), ranging from 1.7 in Type 1 (*Aspidosperma quebracho-blanco* forest) to 5.7 in Type 4 (*Prosopis caldenia* forest) (Table 1). In all the four vegetation types described significant differences in the representation of the different chorotypes were observed (Figure 4C–F). Among all chorotypes, the Southern-brazilian and Chaquenian were the best represented (Figure 4E–F). Type 2 (*Zanthoxylum coco forest*) showed the highest percentage for the Low montane chorotype differing significantly from the other vegetation types ($F_{(3,118)}$ 10.25; $p < 0.001$). The Patagonian chorotype was represented only by a single species, *Descurainia antarctica*, recorded in Type 4 (*Prosopis caldenia* forest), that differed significantly from the other vegetation types ($F_{(3,118)}$ 3.43; $p < 0.019$). The representation of the Exotic chorotype differed significantly among vegetation types ($F_{(3,118)}$ 14.23; $p < 0.001$) showing the highest values in Type 4 (*Prosopis caldenia* forest), while Type 1 (*Aspidosperma quebracho-blanco* forest) showed the lowest values (Figure 4D). The Southern-brazilian and Chaquenian chorotypes differed significantly among the four vegetation types ($F_{(3,118)}$ 8.86; $p < 0.001$; $F_{(3,118)}$ 20.31; $p < 0.001$, respectively). The Southern-brazilian chorotype showed the highest mean percentage value per plot in Type 3 (*Geoffroea decorticans* forest; Figure 4E); while the Chaquenian chorotype exhibited the highest mean percentage per plot in Type 1 (*Aspidosperma quebracho-blanco* forest; Figure 4F).

Vegetation types and their relationship with environmental variables

The ISOMAP ordination (Figure 5) displays the four vegetation woody types observed in Table 1. The variation in species composition among the four types is related to climatic, edaphic and topographic variables (Table 2). Type 4 (*Prosopis caldenia* forest) stands are plotted on the upper right portion of the ordination diagram, associated with higher temperature annual range and seasonality, lower annual precipitation and precipitation of the warmer quarter, and soils with higher fine sand content and lower lime and clay content. The stands of Type 3 (*Geoffroea decorticans* forest) are plotted on the lower right and central portion of the ordination and their floristic differences can be attributed primarily to soil chemistry (Na content) and depth and to a higher precipitation of the driest month; additional floristic differences within this type are re-

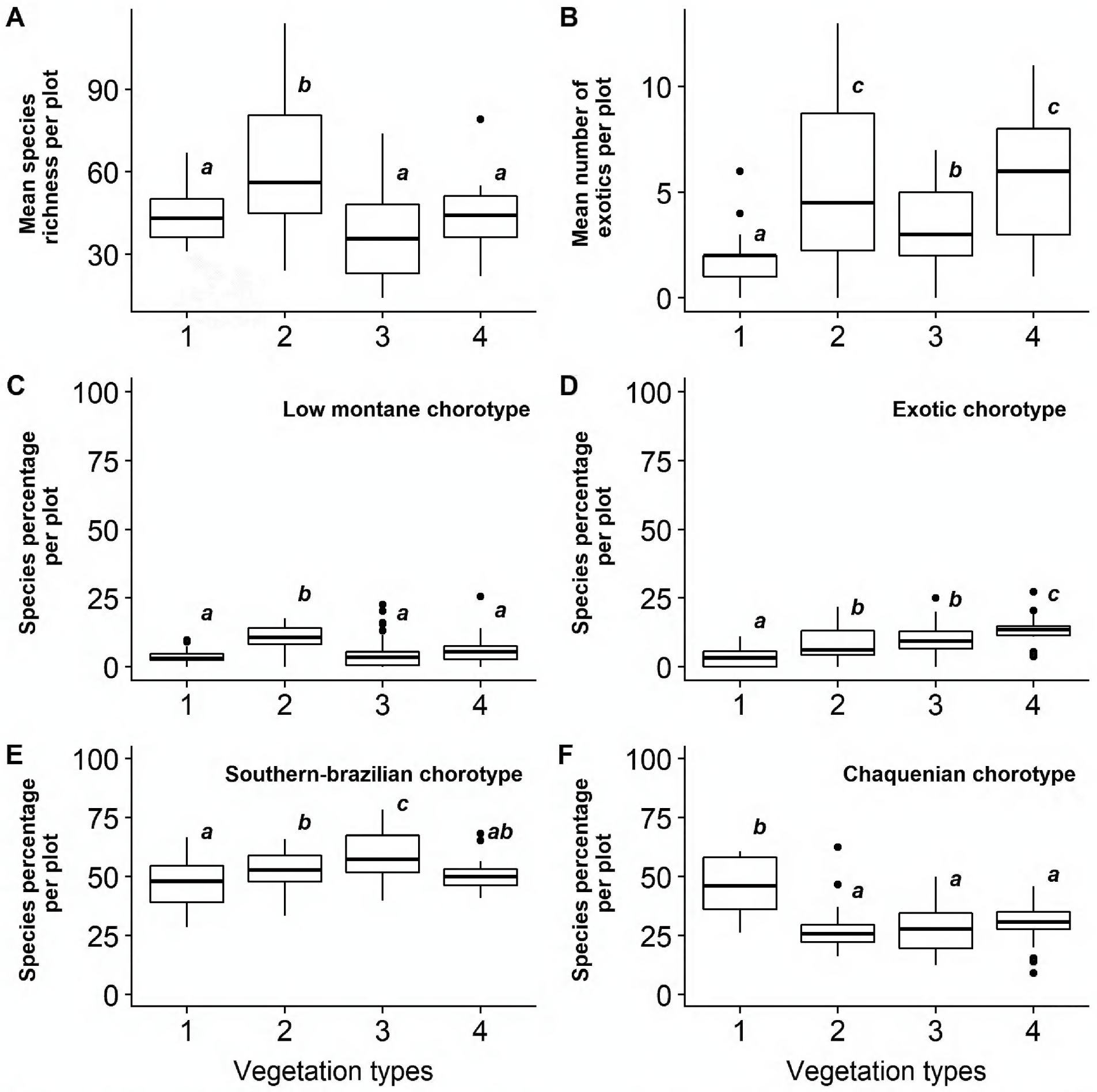

Figure 4. A Mean species richness per plot; **B** mean number of exotic species per plot; **C-F** mean species percentage per plot of different chorotypes for the four vegetation types described in the Espinal phytogeographic province in Córdoba, central Argentina. Vegetation types codes as in Table 1. Different letters indicate significant differences between vegetation types (LSD Fisher, $P < 0.05$).

flected by the dispersion of the stands in the ordination diagram. Stands of Type 2 (*Zanthoxylon coco* forest) are plotted on the left portion of the ordination diagram and its floristic differences are explained by the increase in altitude in the transitional area between true lowland forests and mountain vegetation. Finally, stands of Type 1 (*Aspidosperma quebracho-blanco* forest) are associated with well drained soils with the highest coarse sand content, located in the fluvio-eolian plain in the northern part of the study area. In synthesis, these vegetation types were segregated along gradients of temperature, precipitation, altitude, and of soil-texture and sodium content (Table 2).

Spatial analyses: Espinal extent, current woody vegetation distribution and protected areas

The extent of the Espinal phytogeographic province in the study area, obtained by the overlapping of the previous authors' maps, was 101,550.4 km^2 (Figure 6; Table 3). Further, the comparison of the extent of the Espinal in the overlapped map with previous maps (Figure 6) highlighted the strong differences among authors (Table 3), but the maps by Lewis and Collantes (1973) and Cabido et al. (2018) are most similar (85% similarity) to the Espinal extent used for this study; whereas the maps by the other authors encompass less than 60% (Figure

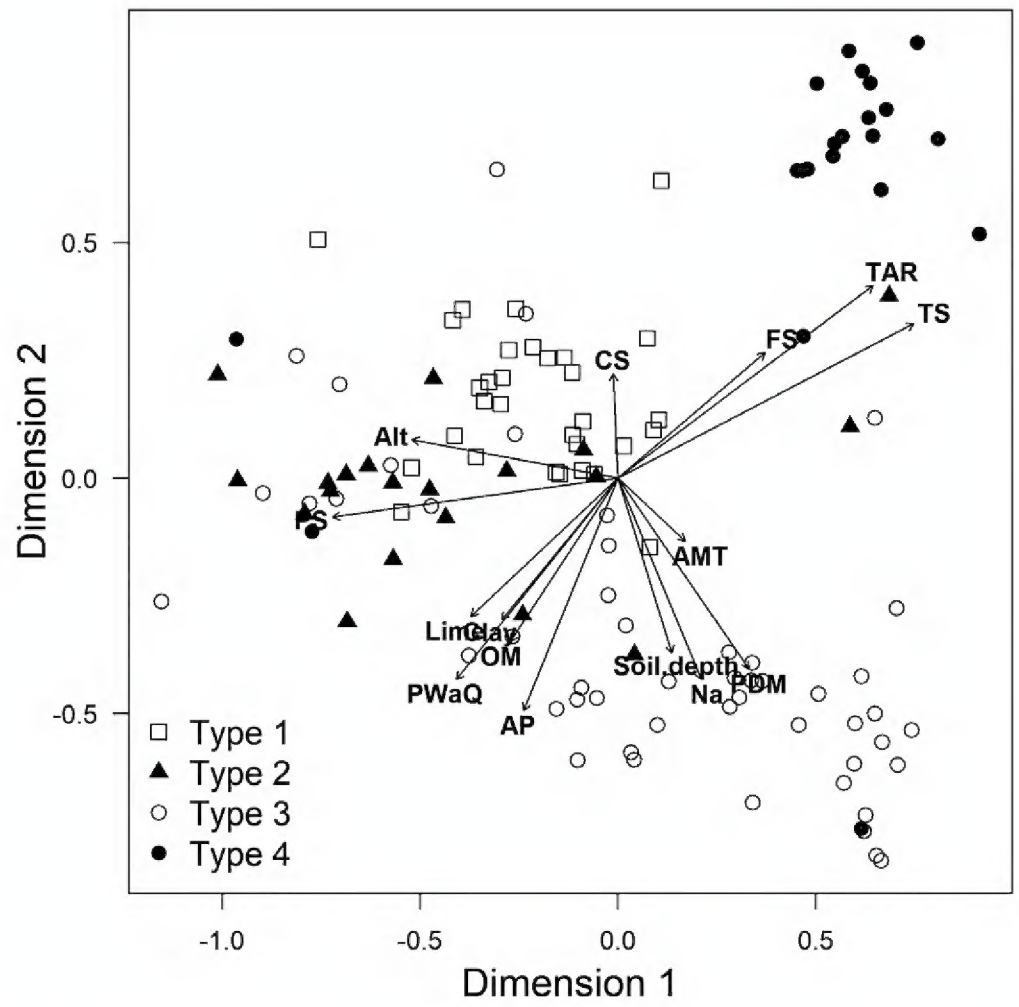

Figure 5. Isometric feature mapping plot (ISOMAP), based on Bray-Curtis dissimilarity of 122 plots × 616 plant species matrix for the Espinal phytogeographic province in Córdoba, central Argentina. Vegetation types codes as in Table 1. Bioclimatic variables with the highest squared correlation coefficient with the sample scores in the ordination space are also reported. Environmental variables: AMT, annual mean temperature; TAR, temperature annual range; TS, temperature seasonality; AP, annual precipitation; PS, precipitation seasonality; PWaQ, precipitation of the warmest quarter; PDM, precipitation of the driest month; Alt, altitude. Edaphic variables: Clay; OM, Organic matter; Soil depth; Na, sodium content; Lime; FS, Fine sand and CS, Coarse sand.

Table 2. Fitted environmental variables onto ISOMAP ordination, reporting their squared correlation coefficient (r^2) and *P*-values based on random permutations of the data. *** and * indicate differences at $p < 0.001$ and $p < 0.05$, respectively.

Environmental variables	r^2
Temperature seasonality (TS)	0.76***
Temperature annual range (TAR)	0.66***
Precipitation seasonality (PS)	0.60***
Precipitation of the warmest quarter (PWaQ)	0.40***
Annual precipitation (AP)	0.34***
Precipitation of the driest month (PDM)	0.31***
Altitude	0.32***
Annual mean temperature (AMT)	0.05*
Lime	0.26***
Fine sand	0.24***
Clay	0.20***
Sodium (Na)	0.26***
Organic matter (OM)	0.22***
Soil depth (SD)	0.18***
Coarse sand	0.07*
pH	0.02

Table 3. Area covered (in km²) by the extent of the Espinal phytogeographic province (i.e. Overlapped map) and maps by previous authors for Córdoba region, central Argentina. Also shown is the percentage of the extent of the Espinal in the maps by different authors with respect to the overlapped map.

Authors	Espinal extent (km²)	Percentage extent
Overlapped map	101,550.41	
Lewis and Collantes (1973)	86,455.08	85.13
Cabrera (1976)	55,013.52	54.17
Cabido et al. (2018)	93,653.23	92.22
Morello et al. (2018)	60,356.74	59.43
Oyarzábal et al. (2018)	57,515.67	56.64

6; Table 3). The map showing the current distribution of the woody patches in the study area showed an overall accuracy of about 97% and a Kappa statistic > 0.92. The vegetation map only shows the general spatial pattern of the woody Espinal relicts, because the different vegetation types lacked distinctive reflectance patterns. The total cover of the current woody patches was 3,483.8 km² (3.43% of the extent of our version of the Espinal phytogeographic province), of which only 1,071.8 km² (31%) are included in the current protected natural areas system.

Discussion

Building on the insights from the previous study by Cabido et al. (2018), the present survey sheds new light on the knowledge of the Espinal forest, recognizing four vegetation types. Moreover, we provide both a map depicting the extent of the Espinal phytogeographic prov-

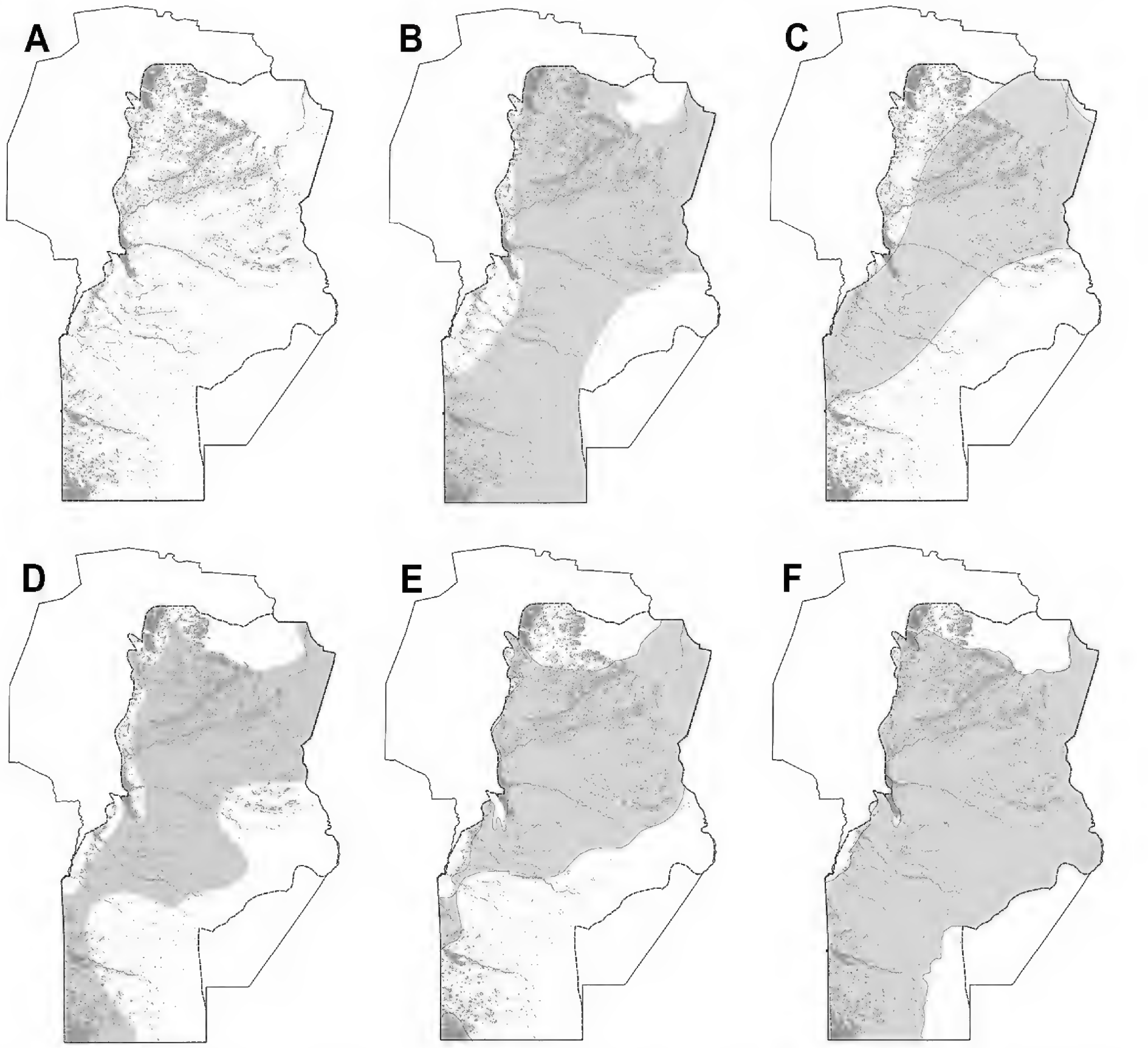

Figure 6. A Overlapped map showing the extent of the Espinal phytogeographic province in Córdoba, central Argentina and the distribution of the current woody vegetation patches; **B-F** Maps of the extent of Espinal in Córdoba by different authors (dark grey): **B** Lewis and Collantes (1973); **C** Cabrera (1976); **D** Morello et al. (2018); **E** Oyarzábal et al. (2018); and **F** Cabido et al. (2018). All maps show the boundaries for the Espinal in the study area resulting from the overlapping of the maps by different authors, together with the current distribution of woody patches.

ince within the study area and an up-to-date map of the current distribution of Espinal forest patches. We should emphasize that the cover of these woody patches represents less than 4% of the extent of the Espinal in Córdoba depicted in both ancient (Cabrera 1953; Lewis and Collantes 1973) and more recent (Cabido et al. 2018; Morello et al. 2018; Oyarzábal et al. 2018) phytogeographic maps. Notwithstanding this dramatic forest loss (Guida-Johnson and Zuleta 2013; Garachana et al. 2018), the representation of the Espinal vegetation types in the current formal system of protected areas is alarmingly low (i.e. 1.05% of the extent of the Espinal in the study area).

Floristic patterns and their relationship with environmental determinants

The changes detected in floristic composition among the four vegetation types are associated mainly to environmental and edaphic variables related to precipitation and temperature seasonality jointly with a soil water availability gradient probably determined by soil texture (i.e. sand, lime and clay content) and sodium content. These conditions vary in the study area in a northeast to southwest direction, in agreement with Matteucci (2018). At the southern extreme of the study area, where the highest temperature oscillation, the lowest precipitation records

and fine sandy soils were registered, the *Prosopis caldenia* forest was identified. Our floristic lists agree with former descriptions and with data reported for La Pampa region, located to the south of our study area (Koutche and Carmelich 1936; Lewis and Collantes 1973). Previous studies have described this vegetation type as "the Pampense" district (Lewis and Collantes 1973) and "the Calden" district (Cabrera 1976; Olson et al. 2001; Oyarzábal et al 2018; Morello et al. 2018). The other three vegetation types share more species among them than with the *Prosopis caldenia* forest and are located under warmer and less dry conditions and on soils with higher clay and lime content. The *Aspidosperma quebracho-blanco* forest, the *Zanthoxylum coco* forest and the *Geoffroea decorticans* forest, were included by Cabrera (1976), Olson et al. (2001), Morello et al. (2018) and Oyarzábal et al. (2018) under the same division ("*Prosopis* district"), while Lewis and Collantes (1973), divided this single unit into six different districts. In the northern part of the study area, *Aspidosperma quebracho-blanco* forest patches are distributed; its identity is determined mainly by species widely distributed in the southern extreme of the Chaco phytogeographic province (e.g. *Aspidosperma quebracho-blanco*, *Prosopis kuntzei*, *Sarcomphalus mistol*, etc.; Sayago 1969). These species confirm the transitional character of the *Aspidosperma quebracho-blanco* forest between the Espinal and Chaco phytogeographic provinces (Cabido et al. 2018). This type shares many species with the *Zanthoxylum coco* forest. The latter is distributed in the western part of the study area, representing a transitional community between the forests on fluvio-eolic sedimentary plains and the low Mountain Chaco Forest (Giorgis et al. 2017; Cabido et al. 2018). Consequently, the diagnostic species group includes several taxa characteristic of the Mountain Chaco Forest district (e.g. *Zanthoxylum coco*, *Lithraea molleoides* and *Croton lachnostachyus*; Cabido et al. 1991; Giorgis et al. 2017), as well as lowland Chaco/Espinal species (e.g. *Condalia buxifolia*; Cabido et al. 2018). Finally, the patches located to the central and eastern sectors of the study area, on soils with the highest sodium content, were classified as the *Geoffroea decorticans* forest. As seen in the ordination diagram in Figure 5, this vegetation type shows additional internal floristic differences partly because of changes in soil drainage and perhaps also due to the influence of differential land use. The dominance of *Geoffroea decorticans* on this vegetation type seems to be promoted by its sprouting roots (Ulibarri et al. 2002) and tolerance to higher sodium soil levels (Karlin et al. 2013). These attributes probably allow *Geoffroea decorticans* to behave as a colonizing species on soils not suitable for agriculture but also over abandoned sites that were previously occupied by forests dominated by *Prosopis alba* and/or *P. nigra* and codominated by *Celtis ehrenbergiana* (Cabido et al. 2018). The advance of *Geoffroea decorticans* over abandoned crop fields was recognized almost 50 years ago by Lewis and Collantes (1973) and more recently by Lewis et al. (2006, 2009). In agreement with these authors and based on our own observations, we predict that perhaps this type will become the dominant vegetation in abandoned fields of the study area if urgent policy measures are not taken into account.

Lewis and Collantes (1973) highlighted the difficulty of differentiating vegetation units within the Espinal based only on the fidelity of species, and they recognized vegetation districts on the basis of physiognomy and the relative abundance of certain dominant plant species. Our results also show that the number of species restricted to a particular vegetation type and, consequently, to be considered as characteristic species (*sensu* Braun-Blanquet 1932) is limited. The small number of exclusive species found could be related to the lack of severe environmental/biogeographic barriers (Bucher 1982), reinforcing the hypothesis stated by Cabrera (1976) concerning the transitional character of the Espinal as an "impoverished Chaco" between the Great Chaco to the north and the Pampas to the south (Bucher 1982). Perhaps as a consequence of the aforementioned lack of barriers to dispersal, a group of ubiquitous species showed high constancy and cover in all four vegetation types (e.g., *Vachellia caven*, *Schinus fasciculatus*, *Setaria lachnea*, and others; see Table 1 and also Suppl. material 2: Table S2.1 for the extended Table 1) and may also explain why the chorotypes Southern-brazilian and Chaquenian are dominant in all the four vegetation types. However, we should not ignore that centuries of human activities (i.e. agriculture and logging; Schofield and Bucher 1986) may have caused the loss and reduction of the range of some characteristic species and, simultaneously, the advance of exotic species that are becoming diagnostic of what we may consider to be "novel ecosystems" (*sensu* Hobbs et al. 2006) with a strong potential to change ecosystem functioning. Another consequence of the intense human activities in the study area is the internal physiognomic heterogeneity observed in all the vegetation types, especially in the *Geoffroea decorticans* forest.

The significant presence of exotic species in the study area has already been reported by different authors (Lewis et al. 2009; Noy-Meir et al. 2012; Cabido et al. 2018). Even though we did not include stands dominated by exotic tree species, a total of 67 exotic taxa, rather evenly distributed (in terms of species richness) among the four vegetation types, were recorded in this study. From a comprehensive list of 40 woody exotic species reported by Giorgis and Tecco (2014) for central Argentina, seven were recorded in this survey. Some of them, such as the trees *Melia azedarach*, *Morus alba* and *Ligustrum lucidum*, showed a high fidelity to the *Zanthoxylum coco* forest. In the same way, the invasive grass *Cynodon dactylon* was identified as a diagnostic species of the *Geoffroea decorticans* forest. Currently, there is general agreement that the advance of exotic species over the Espinal forest is one of the major threats for the conservation of native biodiversity (Lewis et al. 2009; Noy-Meir et al. 2012; Matteucci 2018). The *Prosopis caldenia* forest exhibited the highest mean species richness and proportion of exotics per plot, perhaps because of the

agricultural matrix surrounding these stands since the beginning of the 20th century.

Our floristic survey reported a total of 116 endemic species at the national level, but the number of species restricted only to the study area is almost negligible. Among the highly restricted taxa, *Prosopis caldenia* deserves a special consideration since it is a unique woody species with a very limited range. The conservation status of this species appears as "unspecified" in the Red Lists of the IUCN (http://www.iucn.org); however, its habitat appears to be in "continuing decline in area, extent and/or quality." Delucchi (2006) identifies this species as "vulnerable" due mainly to anthropic activities. Another emblematic taxa recorded in some of the stands sampled in the north and northeast of the study area is the endemic palm *Trithrinax campestris*. Kurtz (1904) and Sayago (1969) reported the high frequency of *Trithrinax campestris* intermingled in forests or in grassland savannas, and Lewis and Collantes (1973) identified a floristic district based in part on the occurrence of this species, but in this study the floristic composition of the patches including *T. campestris* was not clearly differentiated.

Espinal extent, current woody patches distribution and protected areas

Old scientific reports (Lorentz 1876; Kurtz 1904; Frenguelli 1941; Stieben 1946; Cabrera 1953), as well as information compiled from historical documents, oral tradition and more recent contributions (Sayago 1969; Lewis and Collantes1973; Luti et al. 1979), all of them agree in that the Espinal forests dominated the landscape at least until the last decades of the 19th century. From the extent of Espinal province estimated through the overlapped map (ca. 101,500 km^2), a proxy of the potential extent of Espinal forests, only less than 3,500 km^2 (3.43%) of woody patches currently remains. Divergences in the extent of the Espinal phytogeographic province reported by previous authors highlight the difficulties for defining its borders and the need for a comprehensive classification not only for the Espinal vegetation but also neighboring phytogeographic units, such as the Pampa and the Chaco. Regardless of the various phytogeographic maps used to show the comprehensive Espinal extent, it is remarkable that the Espinal woody vegetation has significantly been reduced and fragmented, confirming the dramatic trends for the seasonally dry subtropical forests in South America, already reported by Agost (2015), Cabido et al. (2018) and Garachana et al. (2018).

Finally, our results show that in the study area, the representation of the Espinal forests in formally established natural reserves is almost negligible. The full extent of protected areas comprising well-conserved forest relicts is less than 1,100 km^2 and the figures are even more critical when the whole extent of the Espinal in Argentina is considered (i.e. less than 0.03%; Brown et al. 2006). We should note that these low values are in line with the fact that natural areas developed on flat productive lands have traditionally been excluded from conservation strategies, both at the global (Pressey et al. 2002) and at the regional level (Baldi et al. 2018).

Conclusion

In this study we provide baseline information concerning the floristic heterogeneity and diversity of native forest types of the Espinal forest region in central Argentina. We report four native woody vegetation types segregated along gradients of temperature, precipitation, altitude and soil. Despite the dramatic changes that have taken place since the 19th century, we consider the four vegetation types identified here as representative of the seasonally dry subtropical-warm temperate forests that covered the study area a few centuries ago. Nonetheless, our findings highlight the dramatic reduction in extent and quality of these ecosystems and the need to adopt urgent conservation measures that may stop the conversion of these forests and shrublands to agriculture and grazing lands, as well as the need to take appropriate management actions against invasive exotic species. Recently, the local authorities have established an Agroforestry Plan (Provincial Law 10,467) that compels land owners to plant tree species in at least 2% of their properties in a term of ten years. However, the list of species suggested by the authorities includes exotic trees; whereas, the plan should be restricted to native trees in order to avoid further promoting invasive exotic tree species. The conservation status of the Espinal forests is uncertain and, at this time, its survival depends almost entirely on the good will of private owners. The establishment of new protected areas including the last relicts of these forests should be an essential further step for their conservation.

Author contributions

S.R.Z., M.A.G. and M.R.C. designed the study, S.R.Z., M.A.G., M.R.C. and J.J.C. collected the data; S.R.Z. and M.R.I. performed analyses; S.R.Z., M.A.G. and M.R.C. led the writing; J.J.C. and A.T.A. contributed substantially to revisions.

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Supplementary material

Supplementary material 1
Analytical table with individual relevés (Table S1.1).
Link: https://doi.org/10.3897/VCS/2020/38013.suppl1

Supplementary material 2
Extended synoptic table (Table S2.1).
Link: https://doi.org/10.3897/VCS/2020/38013.suppl2

Supplementary material 3
Species observed and non-parametric estimators species richness for the four vegetation types (Table S3.1).
Link: https://doi.org/10.3897/VCS/2020/38013.suppl3

Supplementary material 4
Mean cover and height with their respectively standard error and maximum and minimum cover values recorded for tree, shrub and herb layers for the four vegetation types (Table S4.1).
Link: https://doi.org/10.3897/VCS/2020/38013.suppl4